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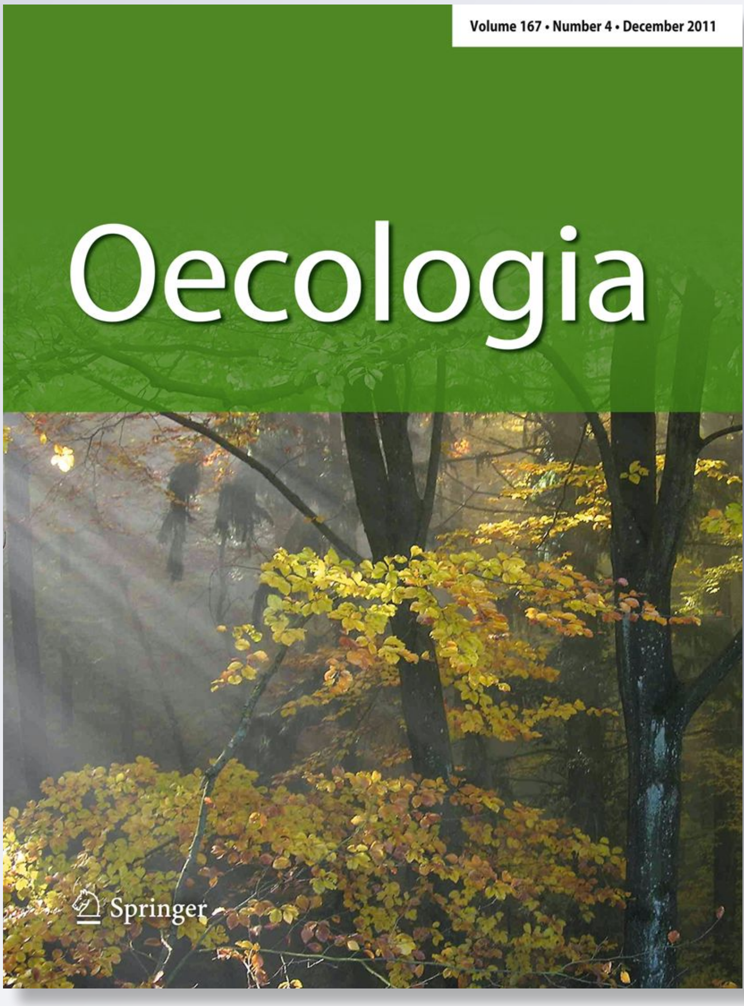

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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Unexpected patterns of sensitivity to drought in three semi-arid grasslands

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Abstract Global climate models forecast an increase in the frequency and intensity of extreme weather events, including severe droughts. Based on multi-year relationships between precipitation amount and aboveground annual net primary production (ANPP), semi-arid grasslands are projected to be among the most sensitive ecosystems to changes in precipitation. To assess sensitivity to drought, as well as variability within the shortgrass steppe biome, we imposed moderate and severe rainfall reductions for two growing seasons in three undisturbed grasslands that varied in soil type and climate. We predicted strong drought-induced reductions in ANPP at all sites and greater sensitivity to drought in sites with lower average precipitation, consistent with continental-scale patterns. Identical experimental infrastructure at each site reduced growing season rainfall events by 50 or 80%, and significantly reduced average soil moisture in both years (by 21 and 46% of control levels, respectively). Despite reductions in soil moisture, ANPP responses varied unexpectedly—from no reduction in ANPP to a 51% decrease. Although sensitivity to drought was highest in the semi-arid grassland with lowest mean annual precipitation, patterns in responses to drought across these grasslands were also strongly related to rainfall event size. When growing season rainfall patterns were dominated by many smaller events, ANPP was significantly reduced by drought but not when rainfall patterns were characterized by large rain events. This interaction between drought sensitivity and rainfall event size suggests that ANPP responses to future droughts may be reduced if growing season rainfall regimes also become more extreme.

Keywords Climate change · Rain event size · Precipitation patterns · Shortgrass steppe · Aboveground annual net primary productivity (ANPP)

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Introduction

Global climate models predict an increase in inter-annual variability in precipitation regimes and more intense and frequent extreme weather and climate events, including multi-year droughts (IPCC 2007; Ray et al. 2008). North American semi-arid grasslands (shortgrass steppe) which cover the western region of the US Great Plains routinely experience seasonal water stress with multi-year droughts common historically (Lauenroth et al. 2008). Thus, the extreme climate of the shortgrass steppe is projected to become even more so in the future. As in many terrestrial and most grassland ecosystems, precipitation has been identified as a primary factor limiting ecosystem processes in semi-arid grasslands, particularly aboveground net primary productivity (ANPP; Sala et al. 1988). Furthermore, these grasslands are considered to be among the most sensitive ecosystems to changes in water availability (Knapp and Smith 2001; Huxman et al. 2004). Therefore, any predicted alterations in climate that may affect ecosystem water balance, including changes in precipitation or warming temperatures, are expected to have significant impacts on ANPP and ecosystem processes in semi-arid grasslands.

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The influence of precipitation on ANPP in grasslands and across biomes in North America has been assessed at both large spatial and long temporal scales (Webb et al. 1978; Sala et al. 1988; Lauenroth and Sala 1992; Knapp and Smith 2001; Huxman et al. 2004). However, most relationships developed are based on *observational data,* either from single sites or multiple sites that span natural precipitation gradients. There are far fewer experimental studies across multiple sites (e.g., Gilgen and Buchmann 2009; Heisler-White et al. 2009). A key limitation to relying on observational data is the lack of control for extrinsic and/or co-varying factors that may influence precipitation–ANPP relationships. Wet years (and sites) may differ in many ways from dry years (and sites) beyond precipitation amount (Gilgen and Buchmann 2009). For example, the average size of precipitation events in wet years is usually larger, events may be more numerous, average temperatures may be lower, cloud cover higher, etc., and previous year's climate and production may influence current year's responses (Webb et al. 1978; Sala et al. 1992; Oesterheld et al. 2001; Wiegand et al. 2004). At present, the role these other factors play in determining responses to drought, in addition to precipitation amount, is unclear.

Experimentally altering precipitation inputs into an ecosystem is a more direct way to assess the sensitivity of ANPP to changes in precipitation (Sala et al. 1988, 1992; Weltzin et al. 2003; Hanson and Wullschleger 2003; Gilgen and Buchmann 2009; Heisler-White et al. 2008, 2009), but such experiments are usually performed at a single site, with the implicit assumption that responses are, to some extent, representative of the biome. Indeed, because sites within biomes share broadly similar climates, plant community composition, and potential meristem limitation constraints (Lauenroth and Sala 1992; Knapp and Smith 2001; Sala et al. 1988), any variation in sensitivity in ANPP to precipitation would be expected to be much less within than across biomes. There are, however, few experimental tests of this prediction.

The objectives of our study were twofold: (1) to directly assess the sensitivity of the shortgrass steppe to experimentally imposed reductions in precipitation amount to test the inference from observational relationships of strong drought sensitivity in this biome, and (2) to evaluate patterns of within-biome drought sensitivity by repeating the experiment at three sites that span different soil types, and a significant portion of the range in mean temperature and precipitation that occurs across this important North American grassland biome. We imposed two levels of growing season rainfall reduction (50 and 80%) for 2 years at these sites, and predicted (1) that significant reductions in ANPP would result at all sites at both levels of drought, and (2), that if differential sensitivity to drought was evident across the three sites, reductions in ANPP (sensitivity) would be greater in drier than wetter sites within the shortgrass steppe, consistent with the continental pattern observed when multiple biomes have been compared across North America (Knapp and Smith 2001; Huxman et al. 2004).

Materials and methods

Study sites

Research was conducted at three sites located along a latitudinal gradient that encompassed much of the north to south extent of the North American semi-arid grassland biome. Representative of the shortgrass steppe biome, the soils at all three sites were Aridic Argiustolls (Kelly et al. 2008) and approximately 60% of root biomass is found in the top 15 cm of soil (Gill et al. 1999). The northern site was located at the Central Plains Experimental Range (CPER) in north-central Colorado (40°49′N, 104°46′W), 61 km northeast of Fort Collins, CO. Experimental plots were located in a site on which cattle grazing had been excluded since 1999. At the CPER, the sandy loam soils (Lauenroth et al. 2008) were the coarsest among sites and the bulk carbon-to-nitrogen ratio was 13.8 (Cherwin, unpublished data). The C_4-grass dominated plant communities at the particular site of our experiment, as well as across the CPER, were dominated by the perennial rhizomatous grass, blue grama [*Bouteloua gracilis* (HBK) Lag. ex Griffiths] with total plant canopy cover averaging 80%. In general, *B. gracilis* accounts for 70% of total canopy cover and 90% of the aboveground biomass of grasses at this site with other grasses, forbs, shrubs, and succulents accounting for approximately 20% of total canopy cover (Table 1; Sala and Lauenroth 1982).

The central site was located at the Sand Creek Massacre National Historic Site, a unit of the National Park Service (NPS), approximately 12 miles east of Eads, CO (38°32′N, 102°31′W). Research plots were located in an area of the park that was used for livestock grazing for nearly 150 years until the NPS acquired the site in 2001 and excluded grazing. Soils at this site had the finest texture and were classified as clay soils with a carbon-to-nitrogen ratio of 6.7. Vegetation canopy cover varied from 65 to 80% at this site with *B. gracilis* also dominant here (85–97% of cover; Table 1).

The southern study site was located at Fort Union National Monument, a former military post also now a unit of the NPS, in northeastern New Mexico (ca. 28 miles N of Las Vegas, NM, 35°91′N, 105°01′W). The semi-arid ecosystem at Fort Union was used extensively in the past (1851–1956) for horse and cattle grazing. However, livestock grazing has been excluded at the site for the past 60 years. This exclusion, along with native grass seeding

Table 1 Description of three study sites along a latitudinal gradient in the semi-arid grassland biome of North America

Site	Mean annual temperature (°C)	Mean annual precipitation (mm)	Elevation (m)	Total cover of grass species (%)	Relative cover of C_4 grasses (%)
North (USDA-ARS CPER)	7.2	342	1,650	64.9	90.5
Central (Sand Creek NHS)	8.3	385	1,219	58.1	99.4
South (Fort Union NM)	9.4	425	2,043	75.6	96.0

Total canopy cover of grasses was heavily dominated by C_4 species, predominantly blue grama [*Bouteloua gracilis* (HBK) Lag. ex Griffiths]. Climate data for the northern site are 69-year means from 1939 to 2008 (USDA-ARS CPER). The central site climate data are 101-year means from 1907 to 2008 (CoAgMet). Climate data for the southern site are 157-year means from 1851 to 2008 (Fort Union National Monument)

and soil conservation efforts beginning in the mid-1970s, has allowed the native ecosystem to recover (Stubbendieck and Willson 1987). Soils at this site were sandy clay loams and had a carbon-to-nitrogen ratio of 8.0. Total vegetation canopy cover is approximately 75% and is dominated by *B. gracilis,* which accounts for roughly 70% of the total canopy cover (Table 1).

Combined these three sites encompassed a N–S gradient in mean annual precipitation from 342 to 425 mm and a mean annual temperature range from 7.2 to 9.4°C (Table 1). Across the entire shortgrass biome precipitation varies from 300 to 600 mm and temperatures from 7.0°C in the north to 16°C in the south (Lauenroth et al. 2008); thus, our three sites, all of which were dominated by *B. gracilis* with similar levels of plant community richness (Table 1), captured a substantial amount of climate variation from the drier, cooler portion of the range of this grassland type.

Rainout shelters

To impose precipitation reductions, 20 passive rain deflection shelters were constructed at each site based on the design of Yahdjian and Sala (2002). The shelters covered 5.6-m^2 plots (2.25 × 2.5 m) and had angled roofs composed of transparent Plexiglas troughs alternating with open areas. Ten shelters were constructed with eleven 2.5-m-long by 11-cm-wide troughs equally spaced and targeted to reduce ambient precipitation inputs by 50%, and 10 were constructed with 18 troughs more closely spaced to reduce precipitation by 80%. Ten control plots, without any infrastructure, received ambient amounts of precipitation. All plots were randomly located in 900-m^2 areas that were flat or with <1% slope and with relatively homogenous vegetation cover and no obvious signs of animal disturbance. Gutters and downspouts were installed on the downhill side of the deflection shelters to drain water away from the target plot and all adjacent plots. All plots were located >1 m from the nearest neighboring plot. Shelters were in place from early June 2007 through November 2007 and from April 2008 through November 2008 thereby creating drought for two consecutive growing seasons.

Volumetric soil moisture content was measured with Decagon soil moisture sensors (ECH$_2$O probes). At each site, half the plots in each treatment (5 per treatment, 15 total) had these sensors placed near the center of the plot. Soil moisture probes were inserted vertically and integrated soil moisture over the top 20 cm of the soil. Measurements were recorded on a data logger every 4 h and averaged to produce daily mean soil moisture content.

We examined the shelter effects on the light environment by measuring transmittance of photosynthetically active radiation (PAR) with a 1-m linear quantum light meter (LI-250A; Li-COR) beneath and outside the shelters at 1200 hours MST under full sun conditions at midseason. Effects on the light environment were small, with the 50 and 80% treatments permitting 92 and 80% transmission, respectively. Similar effects on light transmittance have been documented by other studies using structures designed to manipulate ambient rainfall (Yahdjian and Sala 2002; Heisler-White et al. 2008; Fay et al. 2000). Short-term measurements of air and soil temperature indicated that these were only slightly elevated under the shelters (data now shown), also consistent with effects documented by Yahdjian and Sala (2002).

Vegetation measurements

We quantified ANPP by harvesting all aboveground biomass to just above the root crown in a 0.10-m^2 quadrate from each plot at the end of each growing season. Plant material was placed in a drying oven (60°C) until all biomass was dry (48–72 h), then sorted by species and weighed. Previous year's dead biomass was separated from current year's production based on color and structural changes that are visible after overwintering to allow for accurate estimates of ANPP. This estimate did not include any production by succulents or the woody portions of shrubs, both of which were minor components of total ANPP at these sites. To characterize plant species composition, percent canopy cover by species was visually estimated for four 1-m^2 quadrates in each plot (Daubenmire 1959; Collins 1992). Cover was estimated as the vertical

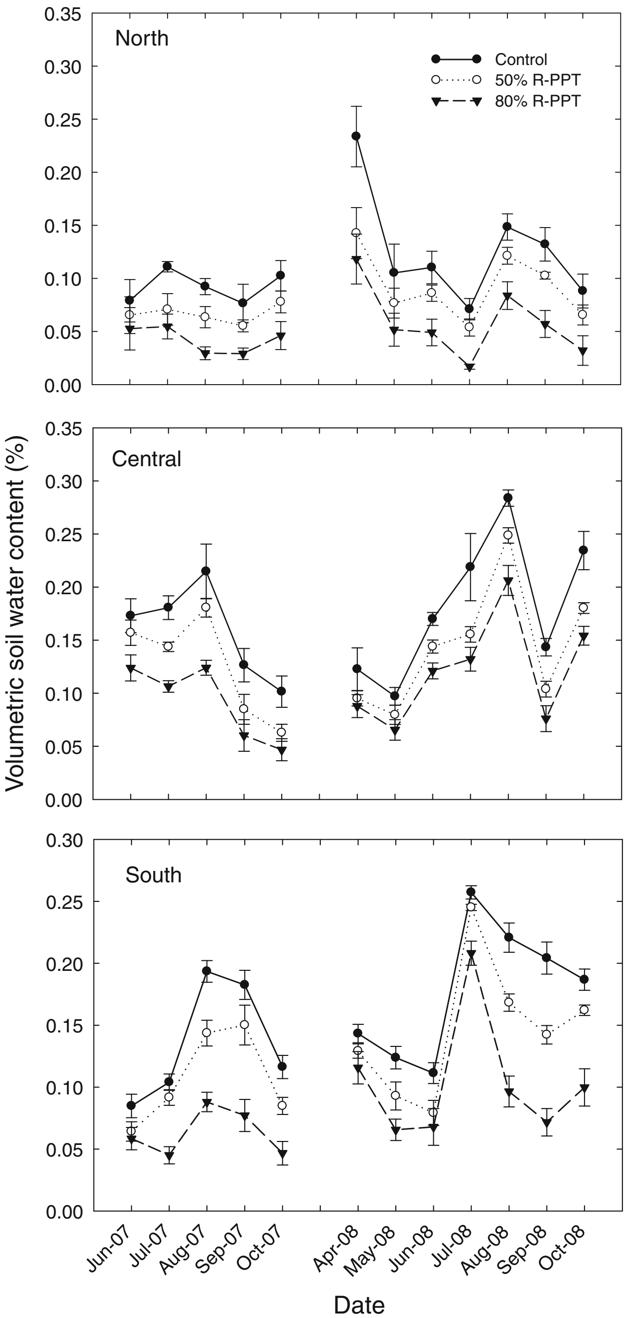

Fig. 1 Dynamics of growing season mean soil moisture (0–20 cm) for ambient and reduced precipitation (R-PPT) experimental plots for 2007 and 2008 at three study sites. Shelters were in place for at least 7 days prior to initial soil moisture measurements. Each *point* represents the monthly mean soil moisture content with *error bars* indicating standard errors calculated from replicate plots for each treatment

projection of a polygon around each plant and projections were summed for each species within a quadrate. Species cover values from the four quadrates were then averaged to obtain the species cover value representative of the plot (see Table 1; and study site description).

Experimental design and analysis

The experimental design was a multi-site randomized complete block design with year as a repeated measure. At each site, 30 plots were organized into 10 blocks to control for any potential within-site variation. The three levels of rainfall interception (0, 50, and 80%) were randomly assigned to plots within each block. A three-factor repeated measures analysis of variance (ANOVA) was used to test for main and interactive effects of site, year, and drought treatment on ANPP and soil moisture. ANPP was $\log_{10}$-transformed to improve symmetry and homogeneity of variance. The model included three fixed effects and their interactions as well as random effects for blocks, nested in sites, and the interaction of treatment within blocks, nested within sites. Computations were performed using the Restricted Maximum Likelihood (REML) method of the MIXED procedure in SAS software version 9.2 (2008, SAS Institute). When main effects and interactions of these factors were detected, we used differences of least squares means (LSMEANS) to compare year and treatment effects within sites. The level of significance was set at $p < 0.05$ for all tests performed, and degrees of freedom were estimated using the Satterthwaite method.

Results

Precipitation regimes

During the course of this 2-year experiment, ambient growing season rainfall regimes varied substantially between sites and years. Growing season rainfall was 224 mm at the northern site in 2007, with rain falling on 43 days and a mean event size of 5.2 mm. In 2008, amounts and patterns were similar with 247 mm of growing season precipitation falling over 39 rain days, and a mean event size of 6.3 mm. Rainfall regimes differed more between years at the central and southern sites. Growing season precipitation was 268 mm (36 days of rain, mean event size of 7.4 mm) in 2007 at the central site but only 185 mm in 2008 (41 rain days, mean event size 4.5 mm). As expected, the southern site received the most growing season precipitation in both years (307 mm in 2007 and 400 mm in 2008). Interestingly, in both years, this site also had the fewest number of rain days (33 in 2007 and 32 in 2008) along with the largest mean event sizes (9.3 mm in 2007 and 12.5 in 2008).

Rainout shelter effects

In spite of these differing rainfall regimes, the rain deflection shelters consistently reduced soil moisture throughout the growing season at all three sites in both years. Although

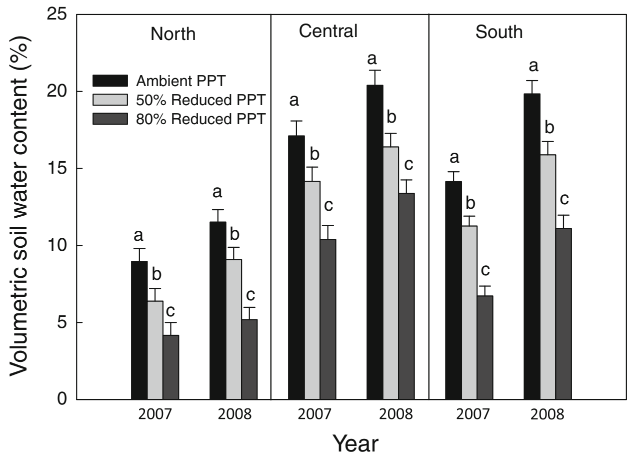

Fig. 2 Mean growing season soil moisture (0–20 cm) for ambient and reduced precipitation (PPT) experimental plots for 2007 and 2008 at three study sites. *Error bars* indicate one standard error and *different letters* represent significant differences ($p < 0.05$) within each site by year combination. Although there was a significant site × year effect (Table 2), those comparisons are not indicated

Table 2 Results from ANOVA for multi-site analysis of drought treatment × site × year for soil moisture and ANPP

Effect	*df*	Soil moisture		ANPP	
		F	*P*	*F*	*P*
Site	2	61.65	<0.0001	723.82	<0.0001
Year	1	90.16	<0.0001	52.29	<0.0001
Site × year	2	6.27	0.0043	66.74	<0.0001
Trt	2	130.92	<0.0001	15.98	<0.0001
Site × Trt	4	1.70	0.1696	10.74	<0.0001
Year × Trt	2	0.64	0.5291	3.71	0.0286
Site × Yr × Trt	4	0.43	0.7877	2.64	0.0380

Note that there were no significant interactions for soil moisture except for site × year, indicating that the drought treatments consistently altered mean soil moisture. In contrast, all interactions were significant for ANPP. Results from site-based analyses for drought treatment × year for ANPP in the northern, central, and southern sites are included in Fig. 3

the 50 and 80% precipitation reductions were not expected to reduce soil moisture by 50 and 80%, differences among the treatments were maintained throughout both growing seasons during both wet and dry periods (Fig. 1; Table 2). Overall, compared to the plots receiving ambient precipitation, the 50% shelters reduced soil moisture by 21% and the 80% treatment caused a 46% reduction across the entire growing season (Fig. 2; Table 2). These patterns of soil moisture reduction among treatments were similar across sites and there were no interactions among site, year, or treatment (Figs. 1, 2; Table 2). Further, even though the same plots were subjected to these treatments for two consecutive years, soil moisture levels in the 2nd year of the drought treatments were typically not lower than in the 1st year, likely because roofs were removed in the dormant season and soil moisture recharge occurred.

Aboveground net primary productivity

Despite consistent reductions in soil moisture at all sites in both years, there was surprising variation in effects on ANPP (Fig. 3; Table 2). At the northern site, ANPP was significantly reduced ($p < 0.05$) in both drought treatments in 2007 and in the 80% treatment in 2008. At the central site, however, there was no significant reduction in ANPP in 2007, but both drought treatments reduced ANPP in 2008. Most unexpected were the lack of ANPP responses to either treatment in either year at the southern site. Thus, the northern site (driest, coolest) was the most sensitive to these imposed growing season precipitation reductions, the central site was intermediate and the southern site (wettest, warmest) was insensitive to these treatments.

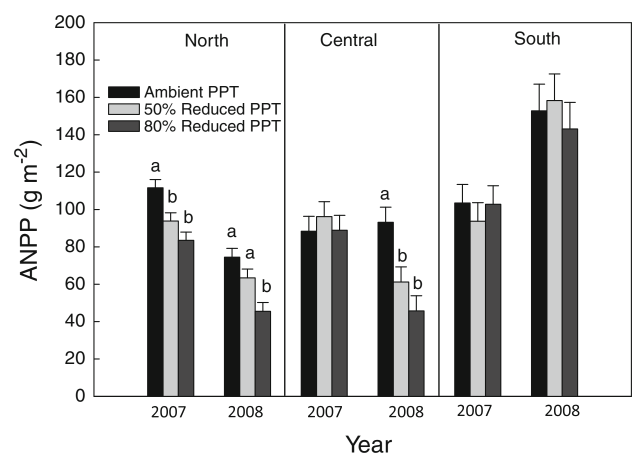

Fig. 3 Total aboveground net primary productivity (ANPP; g m^{-2}) for ambient and the reduced rainfall treatments at the three shortgrass steppe sites. Within each site × year combination, significant treatment differences are represented by *different letters* ($p < 0.05$). See Table 2 for the overall ANOVA results. At the North site, there were significant treatment ($F = 24.29$, $df = 45$, $p < 0.0001$) and year ($F = 112.18$, $df = 45$, $p < 0.0001$) effects; at the Central site, there were also significant treatment ($F = 6.23$, $df = 36$, $p = 0.0048$) and year ($F = 16.72$, $df = 36$, $p = 0.0027$) effects; at the South site there was not a significant treatment effect ($F = 0.19$, $df = 36$, p = NS) but there was a significant year effect ($F = 32.03$, $df = 9$, $p = 0.0003$)

Discussion

Our research was designed to test two predictions: (1) that the semi-arid shortgrass steppe ecosystem would display strong sensitivity (via reduced ANPP) to experimental reductions in precipitation, as inferred from observational analyses, and (2) that variation among sites within the biome would be small, but if there were differential sensitivity to drought, drier sites would be more sensitive than wetter sites, consistent with patterns observed at the cross-biome scale.

Based on previous analyses of observational data (Sala et al. 1988; Lauenroth and Sala 1992; Huxman et al. 2004), the sensitivity of the shortgrass steppe to changes in precipitation [defined as the slope of the ANPP vs. mean annual precipitation (MAP) relationship by Huxman et al. 2004] varies from a maximum of approximately 0.3 g m^{-2} mm^{-1} based on continental scale data (Huxman et al. 2004) to 0.13 g m^{-2} mm^{-1} based on long-term data from the northern site in our study (Lauenroth and Sala 1992). Considering only the three cases in which ANPP did respond to experimental reductions in growing season precipitation (Fig. 3), sensitivity in our study was estimated to be 0.18 g m^{-2} mm^{-1}, more similar to the estimate from Lauenroth and Sala (1992), although the maximum response quantified in our experiment (0.32 g m^{-2} mm^{-1} at the central site) was similar to the estimate by Huxman et al. (2004). However, when all sites and years were considered, these observationally-based estimates of ANPP sensitivity to alterations in precipitation clearly overestimate drought sensitivity. With all six cases combined, the overall sensitivity of ANPP to changes in precipitation was only 0.10 g m^{-2} mm^{-1}, with substantial inter-site and interannual variability (Fig. 3).

The apparent overestimate of ANPP sensitivity to precipitation derived from long-term observations may reflect the importance of other co-varying climatic factors during wet and dry years. Indeed, although the general pattern of differential sensitivity (most sensitive in the drier sites, less so in the wetter) was consistent with larger scale patterns observed across biomes (Knapp and Smith 2001; Huxman et al. 2004), the extreme variation in sensitivity—from no response in ANPP to a 51% reduction was unexpected. Gilgen and Buchmann (2009) reported that there was no consistent grassland response to drought in Switzerland and argued that differences in site management might explain site-specific responses. In our study, however, all three grassland sites were unmanaged. One potential explanation for the overall pattern within this grassland biome would be edaphic gradients from north to south. In these semi-arid grasslands, fine textured soils would be expected to have less plant available water than coarse textured soils (Noy-Meir 1973; Lauenroth and Sala 1992) and, as a result, sites with fine textured soils would be more sensitive to reductions in precipitation. There was no support for this explanation, however, as we detected no consistent relationships between texture (or soil fertility) and drought sensitivity. An alternative explanation for this pattern, consistent with that proposed for continental-scale patterns, is that ANPP in areas with higher amounts of precipitation becomes limited by other resources, and thus such sites are less sensitive to alterations in precipitation (Huxman et al. 2004). This explanation is not supported by the strong variation in interannual ANPP observed at the southern site, however (Fig. 3). While our experimental rainfall reductions did not significantly reduce ANPP at the southern site in either year, greater growing season precipitation in 2008 significantly increased ANPP relative to 2007, suggesting that precipitation amount can and does affect ANPP even at the wettest end of the biome.

We explored a third hypothesis to explain the strong differential sensitivity observed in our experiment—one based on recently documented ANPP responses to alterations in the size of rainfall events in the shortgrass steppe. Sala et al. (1992) argued that large rainfall events, even though they were few in number, were disproportionately important in years with the highest ANPP in the shortgrass steppe. Moreover, recent experiments in which precipitation event size and frequency were altered, but not total amount, showed that fewer but larger growing season rain events led to significantly higher levels of ANPP than precipitation regimes characterized by more frequent, small events (Heisler and Knapp 2008; Heisler-White et al. 2008). Although we did not experimentally vary rainfall event size independently of growing season precipitation amount, for each of our experimental plots we calculated a drought sensitivity index—the ratio of the response in ANPP (control–treatment) divided by the reduction in precipitation for each treatment (ANPP/mm precipitation)—and related this ratio to mean growing season event size (Fig. 4). This analysis revealed a strong inverse relationship between sensitivity to drought and event size. Rainfall patterns characterized by larger events, which have previously been shown to lead to higher levels of soil moisture and ANPP (Heisler-White et al. 2008, 2009), were associated with a lack of ANPP response (insensitivity) to the drought treatments. Mechanistically, we propose that, if rainfall events are sufficiently large, losses of precipitation to evaporation will be minimized, soil moisture will remain at levels permitting growth for extended periods, rain use efficiency will be increased, and for these inherently low production grasslands, ANPP can become uncoupled from precipitation amount (Knapp et al. 2008). Even with proportional reductions in individual event sizes by the shelters, these soil moisture thresholds may have been exceeded by large storms allowing for relatively high levels of ANPP. Overall, these results suggest that there is an important interaction between rainfall regime and sensitivity to changes in precipitation amount in this, and perhaps other, biomes (Leuzinger and Körner 2010), although more direct experimental evidence will be necessary to confirm this. We conclude that, because future climate changes are expected to alter overall ecosystem water balance, total precipitation amounts, and patterns of intra- and interannual

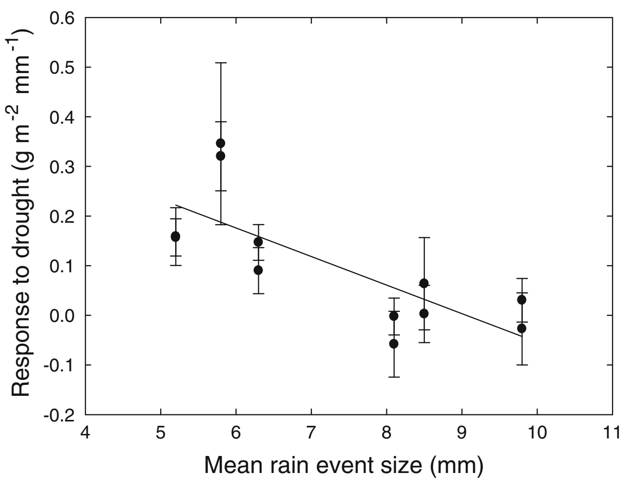

Fig. 4 The relationship between mean rainfall event size during the growing season versus the response (or sensitivity) of ANPP to rainfall reductions ($r^2 = 0.57$, $p = 0.0045$). Sensitivity was calculated at the site level as a ratio of the reduction in ANPP (control–treatment) divided by the reduction in rainfall for each site and year. Both 50 and 80% rainfall reduction treatments are included, and *error bars* represent one standard error of the mean for each year × treatment combination

variability, past observational relationships between mean annual precipitation and ecosystem response may be inadequate for providing insight into future spatial and temporal dynamics of ANPP (Nippert et al. 2006; Knapp et al. 2008).

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